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Comparative analysis of early root system architecture in *Piper nigrum* L. varieties and related *Piper* species

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Abstract

Root system architecture (RSA) helps to understand the plant growth, development, and adaptations. The RSA of *P. nigrum (*Var. Pournami*)*, *P. colubrinum*, *P. chaba*, and 13 *P. nigrum* varieties was studied at the nursery stage to understand variations within and between species. *P. colubrinum* had a robust root system with the highest root length (44.90 ± 7.14 cm) and root spreads (50.23 ± 9.82 cm). Variety, Panniyur-5 (6.70± 0.10 g), recorded the highest root weight, and the longest root was in IISR Malabar Excel (33.10 ± 6.44 cm) and Pournami (32.55 ± 3.75 cm). A significant variation was observed in the number of primary and secondary roots and the number of vessel cells of the varieties. The widest vascular stele was observed in IISR Shakthi (58.73 ± 1.27 µm). The study elucidates variability in roots during the early stages of growth that gives insights of natural adaptations of the *Piper* plants.

Keywords: Root system architecture (RSA), *Piper colubrinum, P. chaba, P. nigrum*

Introduction

The family Piperaceae (pepper family), comprising more than 2,000 species distributed across five genera, is predominantly native to tropical and subtropical regions of the world (Sen & Rengaian, 2022). *Piper colubrinum* Link (Brazilian pepper) is a vigorous species adapted to marshy habitats and is characterized by well-developed prop roots that enhance anchorage under waterlogged conditions. This species exhibits resistance to nematodes and *Phytophthora capsici*, underscoring its importance as a valuable genetic resource for crop improvement (Ro *et al.*, 2022) and as a resistant rootstock (Albuquerque, 1968). *Piper chaba* Hunter (Java pepper) is a flowering climber commonly referred to as the `king of bitters'. This medicinal spice has well-established therapeutic values (Naz *et al.*, 2008; Anyanee & Poomipark, 2020) and is often misinterpreted as 'long pepper' in the local markets. *Piper nigrum* L. (black pepper) is the most important tropical spice crop, hence known as the `king of spices'. It is a perennial tropical vine possessing a taproot system. The commercial propagation of pepper is primarily achieved through stem cuttings and serpentine layering. Consequently, the functional feeder roots of cultivated black pepper plants are predominantly underground adventitious roots arising from the basal stem nodes. Additionally, the plant typically produces 10–15 short adventitious aerial roots that facilitate attachment to support structures. Runner roots develop from the nodes of runner shoots that trail along the soil surface and generally grow perpendicular to the main stem, thereby contributing to lateral root expansion (Parthasarathy *et al.*, 2007).

Black pepper (*Piper nigrum* L.) has more than 1000 cultivars and landraces in the Western Ghats region, which have been extensively characterized for their morphological, biochemical, yield, and resistance attributes (Ravindran, 2000; Prakash *et al.*, 2020). Among the improved cultivars, IISR Thevam and IISR Shakthi exhibit field tolerance to foot rot disease, while Pournami is recognized for its tolerance to root-knot nematodes (Krishnamoorthy& Parthasarathy, 2009). Krishnamurthy *et al.* (2016) reported enhanced root growth in drought-tolerant black pepper accessions, suggesting a potential association between root system architecture and stress adaptation. Comprehensive characterization of tolerant varieties and accessions is therefore essential for effective crop improvement and cultivar development in black pepper. Despite the critical role of roots as the primary organs responsible for water and nutrient uptake, anchorage, and environmental sensing, detailed investigations of root morphological and anatomical traits remain limited. Accordingly, the present study was undertaken to comparatively evaluate the root morpho-anatomical characteristics of selected *P. nigrum* varieties and related species during early developmental stages.

Materials and methods

The study was conducted at the ICAR–Indian Institute of Spices Research (ICAR–IISR), Kozhikode, from January to April 2024. The three species selected for the study were *Piper colubrinum* Link, *Piper chaba* Hunter, and *Piper nigrum* L. (Var. Pournami); Black pepper varieties released by ICAR-IISR, Kozhikode, such as IISR Girimunda, Panchami, Sreekara, IISR Shakthi, IISR Thevam, PLD-2, Shubhakara, Pournami, IISR Malabar Excel, OPKM, and the popular varieties released by Kerala Agricultural University *viz.*, Panniyur-1, Panniyur-5, and Vijay were selected to study the varietal variations.

Root morphological variations

Two-month-old cuttings of all three species and two-month-old serpentine layers of the black pepper varieties were uprooted from the polybags (10 × 8′), and the root fresh weight was taken. The number of primary and secondary roots was counted after placing them in a horizontal panel.

Root anatomical variations

Freehand sectioning of roots (10 cm from the base of the primary roots) was made with the help of a sharp razor blade. The sections were stained with 0.1% Safranin stain and mounted in water (Shethi *et al.*, 2017). For *P. nigrum* varieties, double staining was done with 0.1% Fast Green stain and 0.1% Safranin. The slides were studied under a compound light microscope (Leica DMRB Research Microscope & Euromex iScope IS. 1153- EPL/DF) with a Minolta SLR Camera. Micrographs were taken from various regions of the sections using different magnifications through Motic Image Plus 2.0 software and Image Focus Alpha software. The number of xylem vessels were counted by observing the transverse section of the root taken through the microscope at suitable magnification. The width of the stele was measured using Motic Image Plus 2.0 software and Image Focus Alpha software. The data was recorded in triplicate samples.

Statistical analysis

The experiment was designed in a Completely Randomized Design (CRD) with three replications. The ANOVA of the means was performed at the 0.05 significance level using the RAISINS software 2.20 version (Narwande *et al.*, 2026).

Results and discussion

Comparative root morpho-anatomical features of *Piper* species

The feeder root system of *Piper colubrinum* was robust, woody, and brown in texture, exhibiting a vigorous and extensively spreading architecture characterized by thick, profusely branched adventitious roots. In comparison, *Piper nigrum* developed a dense and highly branched adventitious root system composed of numerous slender roots forming a compact fibrous network. Conversely, *Piper chaba* displayed a comparatively reduced root system, with fewer and thicker roots and limited branching (Figure 1; Table 1). Significant interspecific variation was observed in root length and spread. The greatest mean root length was recorded in *P. colubrinum* (44.90 ± 9.32 cm), followed by *P. nigrum* (32.55 ± 3.75 cm) and *P. chaba* (29.03 ± 3.00 cm). A similar trend was noted for root spread, which was the highest in *P. colubrinum* (50.90 ± 9.98 cm), intermediate in *P. nigrum* (38.10 ± 0.60 cm), and the lowest in *P. chaba* (27.20 ± 1.57 cm) (Table 2). Root biomass also differed among species, wherein *P. colubrinum* had an average root weight of 10.20 ± 5.65 g, followed by *P. chaba* (7.25 ± 0.91 g) and *P. nigrum* (4.06 ± 0.70 g). Despite these differences, the number of primary and secondary roots, as well as the length and spread of primary roots, did not vary significantly during the early stages of development. Anatomical analysis revealed marked variation in stele diameter among species (Figure 2). *P. nigrum* exhibited the widest stele (57.73 ± 1.16 μm), followed by *P. colubrinum* (41.50 ± 1.01 μm) and *P. chaba* (22.43 ± 1.67 μm).

The aerial and subterranean root anatomy of *P. colubrinum*, a species adapted to high-moisture conditions, differed distinctly from that of *P. nigrum*, notably in its less compact stele and smaller pith, consistent with earlier reports (Ravindran & Remashree, 1998). Furthermore, variation between aerial and subterranean roots in *P. colubrinum*, particularly in vascular organization and dicot-like secondary thickening, corroborates previous findings (Kelkar & Krishnamurthy, 1998). The well-developed and extensively branched root system of *P. nigrum* enhances its adaptability to commercial propagation and intensive crop management practices involving regulated irrigation and nutrient supplementation. Although the larger root system of *P. colubrinum* may confer superior nutrient and water uptake capacity, it may also impose a carbon allocation trade-off, potentially limiting assimilate availability for shoot growth (Garnett *et al.*, 2009). Consequently, grafted black pepper plants utilizing *P. colubrinum* as rootstock may require modified production strategies compared with conventional black pepper cultivation. A comparatively robust stele and greater stele diameter observed in *P. nigrum* represent structural adaptations associated with improved drought tolerance, highlighting a potential limitation of *P. colubrinum* as a rootstock species despite its disease resistance advantages.

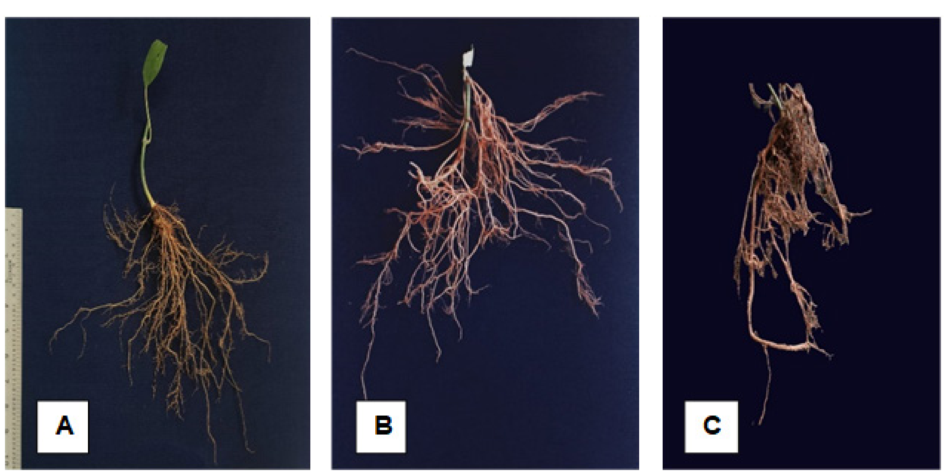

Fig. 1. Adventitious feeder root system of *Piper* species: (A) *Piper nigrum* Var. Pournami (B) *Piper colubrinum* (C) *Piper chaba*

Table 1. Qualitative characteristics of *Pipe*r roots

Character	*Piper nigrum*	*Piper colubrinum*	*Piper chaba*
Type of root	Adventitious	Adventitious	Adventitious
Branching	Highly branched	Very profuse & spreading	Less branched
Root thickness	Slender	Thick	Moderately thick
Root density	Dense	Very dense	Moderate
General appearance	Compact stele with many vascular strands	Stele less compact	Stele broader and more distinct
Cortex	Broad, parenchymatous	Moderately broad	Well-developed and wider
Endodermis	Distinct	Distinct	Distinct
Pericycle	Single layered	Single layered	Single layered
Xylem condition	Highly polyarch (many arms)	Moderate polyarchy	Few but thick xylem arms
Xylem arrangement	Radial, exarch	Radial, exarch	Radial, exarch
Phloem	Alternating with xylem arms	Alternating	Alternating
Conjunctive tissue	Less conspicuous	Moderate	More evident
Pith	Very small or inconspicuous	Small	More distinct and larger
Diagnostic feature	Numerous xylem strands forming dense star	Moderate number of strands	Fewer, thicker vascular strands with a clearer central region

Table 2. Quantitative root morpho-anatomical features of *Piper* species

Species	Root weight (g)	Root length (cm)	Root spread (cm)	No. of. primary roots	Primary root length (cm)	Primary root spread (cm)	No. of secondary root	No. of vessels	Stele width (μm)
P. chaba	7.26 ± 0.91	29.03 ± 3.00^{b}	27.20 ± 1.57^{b}	30.67 ± 12.74	19.87 ± 4.30	14.70 ± 4.20	49.00 ± 9.54	32.67 ± 15.31	22.43 ± 1.67^{c}
P. colubrinum	10.20 ± 5.65	44.90 ± 9.32^{a}	50.90 ± 9.98^{a}	20.33 ± 3.79	30.70 ± 3.98	21.53 ± 18.60	51.67 ± 19.55	55.33 ± 43.88	41.50 ± 1.01^{b}
P. nigrum	4.06 ± 0.70	32.55 ± 3.75^{b}	38.10 ± 0.60^{b}	40.00 ± 21.00	24.97 ± 8.75	14.10 ± 0.52	57.33 ± 4.62	95.33 ±2.52	57.73 ± 1.16^{a}
F stat	2.56^{NS}	5.68*	12.36 **	1.41^{NS}	2.38^{NS}	0.42^{NS}	0.33^{NS}	4.18^{NS}	545.93**
p value	0.16	0.04	0.01	0.31	0.17	0.67	0.73	0.07	0.00

Comparative root morpho-anatomical features of black pepper varieties

The observed morphological variation among *Piper nigrum* varieties at the nursery stage demonstrates significant genotypic diversity in root system architecture (Figure 3). Among the thirteen varieties of *P. nigrum*, Panniyur-5 recorded the highest root weight (6.70 ± 0.10 g), followed by Vijay (6.00 ± 0.50 g), whereas the lowest root weight was observed in Panchami (1.42 ± 0.77 g) and Panniyur-1 (1.42 ± 0.22 g) (Table 3). The longest root was observed in IISR Malabar Excel (33.10± 6.44 cm), which was at par with Pournami (32.55 ± 3.75cm), and the shortest roots were noted in IISR Shakthi (13.40± 5.20 cm) and Shubhakara (15.03 ± 4.05 cm). In contrast, total root spread did not differ significantly among varieties, although numerically higher values were recorded in IISR Malabar Excel (41.60 ± 8.75 cm), IISR Thevam (39.50 ± 8.43 cm), and PLD-2 (38.80 ± 10.93 cm).

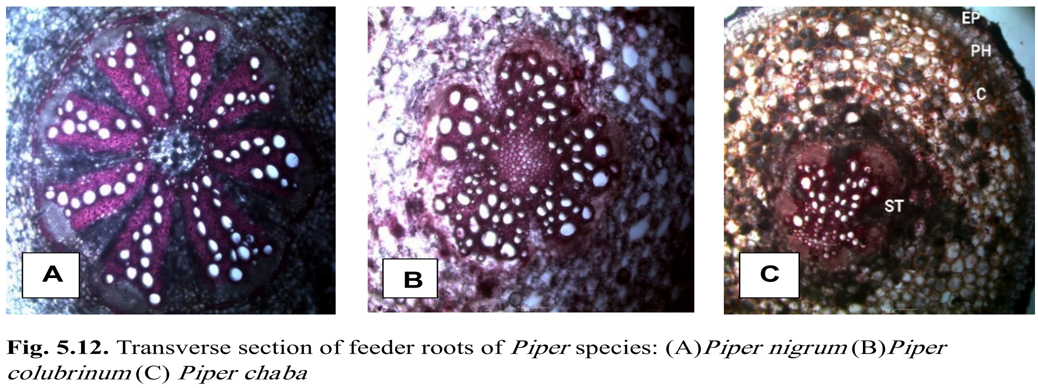

Fig. 2. Transverse section of feeder roots of *Piper* species: (A) *Piper nigrum* (B) *Piper colubrinum* (C) *Piper chaba* (ST-stele, C-cortex, PH- phloem, EP-epidermis)

The highest primary root length was observed in IISR Thevam (27.87 ± 10.15 cm), Pournami (24.97 ± 8.75 cm), and PLD-2 (23.50 ± 13.52 cm), whereas Panniyur-1 (8.63 ± 4.43 cm) exhibited the shortest primary roots. Primary root spread did not vary significantly, indicating relative uniformity in horizontal expansion of primary roots at the nursery stage. A highly significant difference was observed in the number of secondary roots. IISR Thevam (74.67 ± 12.70) and Pournami (57.33 ± 4.62) exhibited profuse secondary branching, whereas Panniyur-5 (17.67 ± 1.53) and OPKM (20.67 ± 13.01) showed comparatively fewer secondary

Fig. 3. The root system of *Piper nigrum* varieties: (A) IISR Girimunda, (B) Panchami, (C) Sreekara, (D) IISR Malabar Excel, (E) IISR Shakthi, (F) Pournami, (G) IISR Thevam, (H) IISR Malabar Excel, (I) Vijay, (J) Panniyur-5, (K) Panniyur-1, (L) PLD-2, and (M, N) OPKM

Table 3. Root morpho-anatomical features of black pepper varieties

Varieties	Root weight (g)	Root length (cm)	Root spread(cm)	No. of. primary roots	Primary root length(cm)	Primary root spread (cm)	No. of secondary root	No. of vessels	Stele width (µm)
IISR Girimunda	3.75 ± 1.89cd	23.43 ± 7.59abcd	25.07 ± 18.88	23.00 ± 5.57	11.57 ± 4.55bc	10.67 ± 2.72	31.00 ± 21.28cdef	74.67 ± 4.51bc	32.53 ± 4.92f
IISR Malabar Excel	4.19 ± 1.90bcd	33.10 ± 6.44a	41.60 ± 8.75	30.33 ± 16.44	20.97 ± 2.25ab	19.33 ± 8.63	42.00 ± 3.61bcd	41.67 ± 8.74e	40.17 ± 2.10cdef
IISR Shakthi	4.72 ± 0.49abc	13.40 ± 5.20d	22.55 ± 12.05	14.50 ± 5.50	19.40 ± 3.46ab	8.87 ± 2.00	44.67 ± 8.02bc	92.33 ± 7.64a	58.73 ± 1.27a
IISR Thevam	3.60 ± 0.24cd	26.87 ± 4.15ab	39.50 ± 8.43	28.33 ± 12.22	27.87 ± 10.15a	15.17 ± 8.31	74.67 ± 12.70a	88.33 ± 13.32a	49.53 ± 5.32abc
OPKM	2.69 ± 2.19de	27.80 ± 2.67ab	33.73 ± 11.45	31.33 ± 4.73	17.70 ± 1.59abc	17.47 ± 11.34	20.67 ± 13.01ef	72.33 ± 7.51c	48.73 ± 0.67bcd
Panchami	1.42 ± 0.77e	23.93 ± 13.76abcd	33.77 ± 21.21	25.67 ± 16.50	18.90 ± 5.17abc	10.50 ± 6.30	39.33 ± 3.79bcde	86.33 ± 7.77ab	44.73 ± 0.92cde
Panniyur-5	6.70 ± 0.10a	21.00 ± 0.05bcd	21.50 ± 0.05	14.00 ± 0.05	18.23 ± 6.51abc	8.63 ± 1.40	17.67 ± 1.53f	58.67 ± 9.87d	39.50 ± 0.36def
Panniyur-1	1.42 ± 0.22e	16.00 ± 4.66cd	21.80 ± 6.92	20.00 ± 4.58	8.63 ± 4.43c	7.70 ± 5.31	22.67 ± 9.45ef	43.00 ± 7.94e	30.90 ± 6.16f
PLD-2	2.78 ± 1.02cde	28.40 ± 9.08ab	38.80 ± 10.93	21.00 ± 2.65	23.50 ± 13.52a	13.73 ± 11.81	41.67 ± 23.54bcd	68.67 ± 2.52cd	44.70 ± 0.96cde
Pournami	4.06 ± 0.70bcd	32.55 ± 3.75a	38.10 ± 0.60	40.00 ± 21.00	24.97 ± 8.75a	14.10 ± 0.52	57.33 ± 4.62ab	95.33 ± 2.52a	57.73 ± 1.16ab
Shubhakara	3.51 ± 1.79cd	15.03 ± 4.05cd	20.67 ± 8.98	30.33 ± 11.68	11.97 ± 3.25bc	4.17 ± 1.15	37.67 ± 3.51cde	43.33 ± 5.03e	38.53 ± 17.81ef
Sreekara	4.31 ± 1.02bcd	25.73 ± 8.08abc	25.63 ± 11.03	39.33 ± 8.33	11.27 ± 0.12bc	8.10 ± 0.87	36.00 ± 6.00cdef	58.00 ± 2.65d	32.03 ± 0.76f
Vijay	6.00 ± 0.50ab	24.80 ± 0.20abc	26.92 ± 0.03	15.02 ± 0.03	21.57 ± 5.44ab	12.03 ± 8.17	25.00 ± 6.08def	59.00 ± 3.00d	45.13 ± 1.07cde
F stat	4.9**	2.8*	1.5NS	2.0NS	2.5*	1.3NS	5.9**	21.3**	7.5**
p value	0.00	0.01	0.19	0.06	0.02	0.29	0.00	0.00	0.00

roots. The number of vessels showed very high statistical significance, indicating big genotypic differences in vascular development. The highest vessel numbers were recorded in Pournami (95.33 ± 2.52), IISR Shakthi (92.33 ± 7.64), and IISR Thevam (88.33 ± 13.32), while IISR Malabar Excel (41.67 ± 8.74) and Panniyur-1 (43.00 ± 7.94) had fewer vessels. Stele width also varied significantly. The widest stele was observed in IISR Shakthi (58.73 ± 1.27 μm) and Pournami (57.73 ± 1.16 μm), followed by IISR Thevam (49.53 ± 5.32 μm) and OPKM (48.73 ± 0.67 μm). The narrowest stele was recorded in Panniyur-1 (30.90 ± 6.16 μm) and Sreekara (32.03 ± 0.76 μm).

Sreekara and IISR Thevam show structured, symmetrical root systems with good horizontal expansion. PLD-2 exhibits thicker primary roots with relatively longer laterals but less fine branching compared to highly fibrous types. IISR Shakthi, IISR Malabar Excel, Panniyur-5, and OPKM have reduced lateral spread, fewer secondary branches, more compact root clusters, and lower overall root biomass. Panniyur-5 and OPKM particularly show limited branching and a comparatively narrow spatial distribution. The OPKM samples demonstrate slender primary roots with minimal lateral proliferation, indicating restricted soil volume occupancy at the nursery stage.

Varieties such as Pournami, IISR Thevam, and IISR Shakthi combined vigorous branching with enhanced vascular development, suggesting superior absorptive and conductive potential. In contrast, Panniyur-1 and Panchami exhibited relatively reduced root development. These findings highlight the existence of considerable genetic diversity in early root system architecture among black pepper varieties, which may influence establishment efficiency, nutrient acquisition capacity, and stress adaptability. The greater number of secondary roots or lateral roots is essential for the spread of roots, which is necessary for the uptake of water and nutrients (Dubrovsky *et al.*, 2019). In organic or low-input environments, genotypic variability in root characters can improve nutrient uptake and the overall performance of the plant (Andresen *et al.*, 2016).

Varieties such as IISR Shakthi, Pournami, and IISR Thevam exhibited a comparatively compact cortex and a well-developed stele with numerous, large, and radially arranged xylem vessels, indicating enhanced vascular differentiation and potentially greater hydraulic conductivity. In contrast, Panniyur-1, Shubhakara, and OPKM displayed relatively narrower steles, fewer and smaller xylem vessels, and a comparatively broader cortex with loosely arranged cells (Figures 4 & 5).

Root growth rate, branching dynamics, and spatial configuration are modulated in response to soil physical, chemical, and biological factors throughout the cropping season (Lynch, 1995). Observations recorded at advanced developmental stages or at physiological maturity may not adequately elucidate the functional relationship between root system architecture (RSA) and plant growth, as root systems exhibit continuous developmental plasticity. Therefore, characterization of RSA during early developmental stages, particularly under nursery conditions, provides a more precise framework for understanding genotype-specific establishment strategies and predicting rootstock performance in black pepper.

Root anatomical traits also influence varietal differences in pathogen susceptibility. Raghavan *et al.* (2010) reported distinct structural differences between Phytophthora-resistant and tolerant black pepper varieties. Anatomical adaptations within the vascular cylinder further contribute to functional resilience under fluctuating environmental conditions. The size and number of xylem vessels are particularly important in determining hydraulic conductivity and resistance to environmental stress, including drought (Kadam *et al.*, 2015). Wider vessels may enhance water transport efficiency, whereas narrower vessels may confer greater safety against cavitation under water-limited conditions.

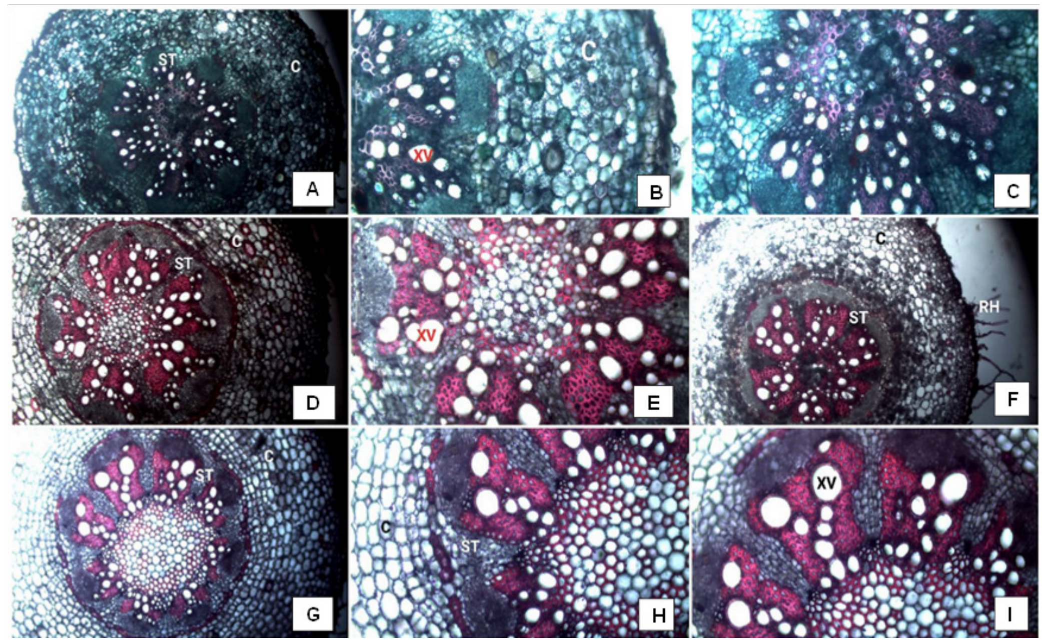

Fig. 4. Transverse sections of feeder roots of *Piper nigrum* varieties: (A) IISR Girimunda, (B) IISR Girimunda 10X, (C) IISR Girimunda 10X, (D)Panchami 5X, (E) Panchami 10X, (F) Sreekara 5X, (G) IISR Malabar Excel 5X, (H) Vijay 10X, and (I) Vijay 10X (C-cortex, ST-stele, XV-xylem vessel)

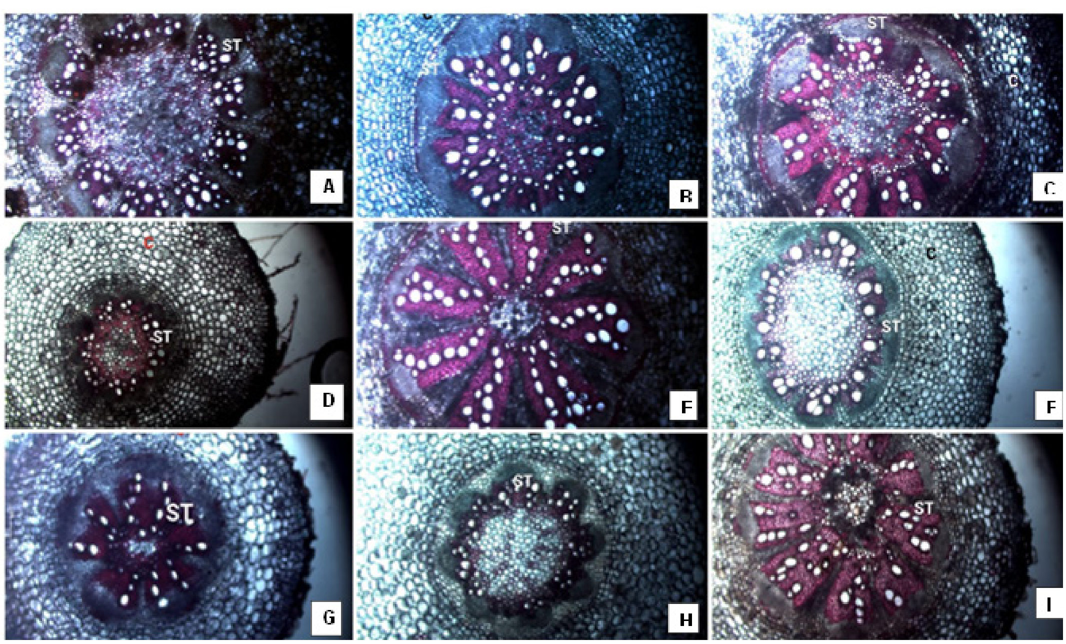

Fig. 5. Transverse sections of feeder roots of *Piper nigrum* in 5X; (A) IISR Shakthi, (B) IISR Thevam, (C) PLD-2, (D) Shubhakara, (E) Pournami, (F) IISR Malabar Excel, (G) Panniyur-1, (H) Panniyur-5 and (I) OPKM (C-cortex, ST-stele, XV-xylem vessel)

Conclusion

Root system architecture (RSA) is a key determinant of water and nutrient acquisition, directly influencing plant establishment and early vigor. Owing to its developmental plasticity and strong environmental responsiveness, RSA must be evaluated at specific growth stages to capture meaningful functional variation. In this study, destructive sampling enabled the precise quantification of early developmental variations of *Piper* roots. A detailed understanding of these structural traits not only enhances varietal characterization but also supports breeding strategies aimed at improving resource-use efficiency and stress resilience. Given the increasing pressures of climate change and limited water and nutrient availability, the incorporation of root architectural traits as a targeted breeding objective will be critical for developing sustainable and high-performing black pepper cultivars.

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